A FURTHER NOTE ON THE BIOMETRICAL ANALYSIS OF QUANTITATIVE INHERITANCE

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Introduction

In a recent paper (2) the senior author proposed a new design-called APBIB design and an alternative approach *for* the estimation of the genetic variances D and H as defined in Mather (1949) in the studies of quantitative inheritance. In this paper we shall present some numerical examples to compare the effeciency of the senior author's method with that of K. Mather (1949).

The APBIB design and the Author's approach

In this section we give a brief account of the APBIB design and the computational procedures of the senior author's approach. As in (2) we shall confine ourselves to experiments involving the F_3 lines, the F_2 individuals and the parents and/or F_1 individuals.

As noted in (2), the APBIB design is in essence a group-divisible PBIB design with two associates for the F_3 lines and the F_2 individuals, combined with a randomized complete block design for the parents and/or F_1 individuals (called augmented lines). For illustration, suppose that we engage *bar* F_2 individuals and ba_1 F_3 lines each line with r individuals in an experiment of b blocks, each block with a_1+a+p plots and each plot with r individuals. Then in actually carrying out the experiment the first step would be to divide in a random manner the F_3 lines and the F_2 individuals into b groups, each group with a_1 F_3 lines and ar F_2 individuals; as a next step each group is allocated at random to one and only one of the blocks, with the F_3 lines occupying a_1 plots and the F_2 individuals occupying a plots. The design is then completed

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by adding p augmented lines (P_1 and P_2 and/or F_1's) to each block to occupy the remaining p plots and randomizing the order of the plots to make the usual hypothesis tests valid. In such a layout it is apparent that any two F_2 or F_3 individuals in the same block appear together in one and only one block, while any two F_2 or F_3 individuals in different blocks do not appear together in any block. Notice further that when an APBIB design is adopted, the following advantages can readily be observed:

(a) It is less restrictive concerning the number of F_3 lines so that the sampling error due to segregation may be reduced to some extend.

(b) It may control the soil heterogeneity more effectively without increasing the size of the block while at the same time, the size of the plot may relatively be enlarged to control the sampling error of segregation in the F_3 lines.

(c) It renders the usual least square method as an effective procedure for estimating the genetic values of the individuals.

Adopting the APBIB design we now proceed to illustrate the principal proceedures of the senior author's approach for the estimation of the genetic variances D and H as defined by Mather (1949). Such an approach as given in this paper is based on the adoption of a fixed model without genetic and environment interaction, as was noted in (2).

(a) Let $Y_{j(1)}$ and $Y_{j'(2)}$ denote the jth F_2 and the j'th F_3 individuals respectively, $j=1, 2 \ldots bN_{F_2}$; $j'=1, 2 \ldots bN_{F_3}$. If $Y_{j(1)}$ and $Y_{j'(2)}$ appear in the ith and the i'th blocks respectively, then the adjusted observations $Q_{F_2 j}$ and $Q_{F_3 j'}$ of $Y_{j(1)}$ and $Y_{j'(2)}$ respectively are obtained as:

$$Q_{F_2 j}=Y_{j(1)}-\bar{B}_{i\cdot},$$
$$Q_{F_3 j'}=Y_{j'(2)}-\bar{B}_{i'\cdot},$$

where $\bar{B}_{i\cdot}$ is the grand average of the ith block, $i=1, 2 \ldots b$.
Similarly we obtain the adjusted value $Q_{c\,j''}$ of the j''th augmented line as

$$Q_{c\,j''}=\sum_{i=1}^{b}\sum_{k=1}^{r}Y_{i\,j''\,k(3)}-br\bar{Y}\ldots,\quad j''=1, 2, \ldots p,$$

where $Y_{i\,j''\,k(3)}$ is the observed value of the kth individual of the j''th augmented line in the ith block and $\bar{Y}\ldots$ is the grand average.

(c) Using the adjusted observations of the F_2 and the F_3 individuals as well as the adjusted values of the augmented lines, we obtain the estimates of the genetic values of the F_2 and the F_3 individuals and the augmented lines as follows: The estimate $\hat{C}_{j''}$ of the genetic value of the j''th augmented line is obtained as $Q_{c\,j''}/rb$. Denoting by $T_{F_3 i}$ and $T_{F_2 i}$ the sums of the adjusted observations of the F_3 and the F_2 individuals respectively in the ith block and

by T_c the sum of adjusted values of all augmented lines, we obtain the estimates $\hat{f}_{2j}$ and $\hat{f}_{3j'}$ of the genetic values of $Y_{j(1)}$ and $Y_{j'(2)}$ respectively as

$$\hat{f}_{2j}=Q_{F_2j}+\frac{1}{rp}(T_{F_2i'}+T_{F_3i'}+\frac{1}{b}T_c),\ j=1,\ 2\ldots bN_{F_2}$$

and $$\hat{f}_{3j'}=Q_{F_3j'}+\frac{1}{rp}(T_{F_2i}+T_{F_3i}+\frac{1}{b}T_c),\ j'=1,\ 2\ldots bN_{F_3},$$

provided that $Y_{j(1)}$ and $Y_{j'(2)}$ appear in the ith and the i'th blocks respectively.

(c) Based on the estimates of the genetic values of the F_2 and the F_3 individuals as given in (b), the corresponding statistics of Mather $V_{F_2(c)}$, $V_{\bar{F}_3(c)}$ and $\bar{V}_{F_3(c)}$, are obtained, with the estimate $\hat{\sigma}^2$ of σ^2 being given in the usual analysis of variance table (Table 2. 1).

Table 2. 1. *Analysis of Variance Table*

Sources of variation	*d.f.*	Sum of Squares	Mean Squares	Expectation
Due to adjusted values of F_2, F_3 and parents and/or F_1:	$df_1=b(N_{F_2}+N_{F_3})+p-1$	$SS_1=\sum_{j=1}^{bN_{F_2}}\hat{f}_{2j}Q_{F_2j}+\sum_{j'=1}^{bN_{F_3}}\hat{f}_{3j'}Q_{F_3j'}+\sum_{j''=1}^{p}\hat{c}_{j''}Q\hat{c}_{j''}$		
Blocks	$df_b=b-1$	$SS_B=N\sum_{i=1}^{b}(\bar{B}_{i\cdot}-\bar{Y}\ldots)^2$		
Residual	$df_e=p(rb-1)-b+1$	$SS_e=SS_T-SS_1-SS_B$	$SS_e/df_e=\hat{\sigma}^2$	σ^2
Total	$bN-1$	$SS_T=\sum_{ijk}Y_{ijk}^2-\frac{\bar{Y}^2\ldots}{bN}$		

where, $N=N_{F_2}+N_{F_3}+pr$

(d) Finally the estimates of D, H and σ^2 are obtained by solving the following equations:

$$\begin{cases}\frac{9}{8}D+\frac{3}{8}H+(\frac{1}{2}+K_1+K_2)\sigma^2=V_{F_2(c)}+V_{\bar{F}_3(c)}+\frac{1}{2}\bar{V}_{F_3(c)}\\ \frac{3}{4}D+\frac{21}{64}H+(K_1+\frac{1}{4}K_2+\frac{1}{2})\sigma^2=V_{F_2(c)}+\frac{1}{4}V_{\bar{F}_3(c)}+\frac{1}{2}V_{F_3(c)}\\ \frac{1}{2}(K_1+\frac{1}{2}K_2+\frac{1}{2})D+\frac{1}{4}(K_1+\frac{1}{4}K_2+\frac{1}{2})H+(K_1^2+K_2^2+2)\sigma^2\\ \quad=K_1V_{F_2(c)}+K_2V_{\bar{F}_3(c)}+\bar{V}_{F_3(c)}+\hat{\sigma}^2,\end{cases}$$

where $$K_1=1+\frac{N_{F_2}}{rp(bN_{F_2}-1)}(b-1),$$

$$K_2=\frac{p(a_1b-1)+a_1(b-1)}{rp(ba_1-1)}$$

where $N=N_{F_2}+N_{F_3}+rp$

Numerical Examples

For the comparison of the senior author's approach with that of Mather (1949) as regards the estimation of the genetic variances D and H, three numerical examples were generated using the parameters given in Table (3. 1)

Table 3. 1. *The relevant parameters for the generation of the three numerical examples*

Ex. I	Ex. II	Ex. III
$\mu=0$ $d_a=d_b=0.5$ $h_a=h_b=0.3$	$\mu=0$ $d_a=d_b=5$ $h_a=h_b=3$	$\mu=0$ $d_a=d_b=0.5$ $h_a=h_b=0.3$
$e\sim$NID(0, 9)	$e\sim$NID(0, 1)	$e\sim$NID(0, 1)
$b_1=4,\ b_2=3,\ b_3=2,\ b_4=1$ $b_5=-1,\ b_6=-2,\ b_7=-3,$ $b_8=-4$	$b_1=10,\ b_2=8,\ b_3=6,\ b_4=4$ $b_5=2,\ b_6=0,\ b_7=-2,$ $b_8=-4$	$b_1=10,\ b_2=8,\ b_3=6,\ b_4=4$ $b_5=2,\ b_6=0,\ b_7=-2,$ $b_8=-4$
$N_{F_2}=32,\ p=4,\ r=16$ $N_{F_3}=64,\ a=2,\ a_1=4$	$N_{F_2}=32,\ p=4,\ r=16$ $N_{F_3}=64,\ a=2,\ a_1=4$	$N_{F_2}=32,\ p=4,\ r=16$ $N_{F_3}=64,\ a=2,\ a_1=4$
P_1; AABB$=d_a+d_b=1.0$ P_2; $aabb=-d_a-d_b=-1.0$	P_1; AABB$=d_a+d_b=10$ P_2; $aabb=-d_a-d_b=-10$	P_1; AABB$=d_a+d_b=1.0$ P_2; $aabb=-d_a-d_b=-1.0$

and employing a fixed effect model, the random errors e being taken from the random normal deviates. These examples were generated according to the following rules:

(a) In generating these examples we assume a fixed effect model as given by

$$F_2;\ Y_{ij(1)}=\mu+b_i+f_{2j}+e_{ij(1)},$$
$$F_3;\ Y_{ij'(2)}=\mu+b_i+f_{3j'}+e_{ij'(2)},$$

and parents; $Y_{ij''k(3)}=\mu+b_i+c_{j''}+e_{ij''k(3)}$, $i=1, 2\ldots b$; $j=1, 2\ldots bN_{F_2}$; $j'=1, 2\ldots bN_{F_3}$; $j''=1, 2\ldots p$; $k=1, 2\ldots r$,

where $Y_{ij(1)}$ denotes the observation of the jth individual of F_2 in the ith block; $Y_{ij'(2)}$, the obseration of the j'th individual of F_3 in the ith block; $Y_{ij''k(3)}$, the observation of the kth individual of the j''th augmented line in the ith block; f_{2j}, $f_{3j'}$ and $c_{j''}$ denote, respectively, the genetic values of the jth F_2 individual, the j'th F_3 individual and the j''th augmented line; μ is the unknown population mean and b_i, the effect of the ith block, $i=1, 2\ldots b$. Notice that

$Y_{ij(1)}$ and $Y_{ij'(2)}$ may or may not exist depending on whether or not the jth F_2 and the j'th F_3 individuals appear in the ith block.

Notice further that, since the estimates given in section two are derived under the restriction $\sum_{j}^{bN_{F_2}} f_{2j} + \sum_{j'}^{bN_{F_3}} f_{3j'} + br\sum_{j''=1}^{p} c_{j''} = 0$, the estimates of the genetic values in these examples are actually the estimates of the deviates of the true genetic values from $\bar{f} = \frac{1}{b(N_{F_2}+N_{F_3}+rp)}\left(\sum_{j}^{bN_{F_2}} f_{2j} + \sum_{j'}^{bN_{F_3}} f_{3j'} + br\sum_{j''=1}^{p} c_{j''}\right)$.

(b) The random variable e were taken at random from "A Million Random Digits with 10,000 Normal Deviates" of the Rand corporation, published by the Free Press publishers, Glencoe, Illinois, USA. It follows that $e\sim$MID(0, 1), as in examples 2 and 3. In example 1 we multiply each "e" by 3 to yield $e\sim$MID(0, 9). In this paper we do not intend to reproduce the observed values of these e's because there are altogether 1200 e's in each example, which would take up a big space for printing.

(c) The parameters f_{2j} and $f_{3j'}$, $j=1, 2\ldots bN_{F_2}$, $j'=1, 2\ldots bN_{F_3}$, were obtained on the supposition of two independent loci, denoted by A—a and B—b, of equal effects and each with two alleles. Hence, given that the additive effects A of—a and B—b be denoted by d_a and d_b respectively while the dominant effects of A—a and B—b by h_a and h_b respectively, we obtain the genetic values (f's) of the various genotypes as given in Table (3. 2).

Table 3. 2. *The genetic values (f_{2j} and $f_{3j'}$'s) of various genotypes in the F_2 and F_3 individuals*

AABB d_a+d_b	AAB*b* d_a+h_b	AA*bb* d_a-d_b
A*a*BB h_a+d_b	A*a*B*b* h_a+h_b	A*abb* h_a-d_b
*aa*BB $-d_a+d_b$	*aa*B*b* $-d_a+h_b$	*aabb* $-d_a-d_b$

(d) Since our interests are centered on the comparison of the senior author's method with that of Mather as regards the estimation of D and H, we purposely allocate the numbers of the F_2 individuals, the F_3 lines and the F_3 individuals in each line to the various genetypes in accordance with the segregation rule as given in tables 3. 3 and 3. 4. Under such an allocation of the number of the F_2 and the F_3 individuals, it is clear that the disturbing effect of the sampling error due to segregation is completely eliminated. In table 3.3 the upper figure denotes the F_2 genotype while the lower figure, the number of F_2 individuals with the indicated genotype in each block.

Table 3. 3. *The allocation of the number of F_2 individuals to various genotypes in each block*

	B−*b*		
V−*a*	AABB 2	AAB*b* 4	AA*bb* 2
	A*a*BB 4	A*a*B*b* 8	A*abb* 4
	*aa*BB 2	*aa*B*b* 4	*aabb* 2

Table 3. 4. *The allocation of the F_3 individuals to various genotypes in the F_3 lines*

Genotype of F_2 parent	Genotypes and their frequencies of F_3 individuals in F_3 lines
AABB AA*bb* *aa*BB *aabb* } each with 2 F_3 lines	AABB 16 AA*bb* 16 *aa*BB 16 *aabb* 16
A*a*BB A*abb* AAB*b* *aa*B*b* } each with 4 F_3 lines	AABB 4, A*a*BB 8, *aa*BB 4 AA*bb* 4, A*abb* 8, *aabb* 4 AABB 4, AAB*b* 8, AA*bb* 4 *aa*BB 4, *aa*B*b* 8, *aabb* 4
A*a*B*a* with 8 F_3 lines	AABB 1, A*a*BB 2, *aa*BB 1 AAB*b* 2, A*a*B*b* 4, *aa*B*b* 2 AA*bb* 1, A*abb* 2, *aabb* 1

Using the generated data we now proceed to obtain the estimates $\hat{D}$ and $\hat{H}$ of D and H by employing the Mather's method as well as the senior author's method. For this purpose we give the relevant quantities in Table 3. 5.

In the Mather's approach, the estimates $\hat{D}$ and $\hat{H}$ are obtained by solving the following set of equations using the ordinary least square method

$$\begin{cases} \frac{1}{2}D+\frac{1}{4}H+E_1=V_{F_2} \\ \frac{1}{2}D+\frac{1}{16}H+E_2=V_{F_3} \\ \frac{1}{2}D+\frac{1}{8}H+E_3=\bar{V}_{F_3} \\ E_1=V_{E_1} \\ E_2=V_{E_2} \\ E_3=V_{E_3} \end{cases}$$

Table 3. 5. *Mather's statistics based on (1) the original observations and (2) the estimated genetic values of the F_2 and the F_3 individuals*

		Ex. I	Ex. II	Ex. III
Mather's statistics based on the original observations	V_{F_2}	16.788	54.528	23.209
	$V_{\bar{F}_3}$	8.407	44.949	21.588
	$\bar{V}_{F_3}$	9.266	16.602	1.210
	V_{E_1}	17.877	21.897	21.747
	V_{E_2}	9.436	22.291	22.062
	$\bar{V}_{E_3}$	9.555	0.960	1.040
Mather's statistics based on the estimated genetic values of the F_2 and the F_3 individuals	$V_{F_2(c)}$	9.700	32.344	1.446
	$V_{\bar{F}_3(c)}$	0.708	27.132	0.314
	$\bar{V}_{F_3(c)}$	9.184	16.641	1.212
	$\hat{\sigma}^2$	9.846	1.301	1.038

$\hat{\sigma}^2$ is obtained from the usual analysis of variance table.

If we write the above as $X\underline{\theta}=\underline{Z}$, where

$$X=\begin{pmatrix} \frac{1}{2} & \frac{1}{4} & 1 & 0 & 0 \\ \frac{1}{2} & \frac{1}{16} & 0 & 1 & 0 \\ \frac{1}{4} & \frac{1}{8} & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}, \quad \underline{\theta}=\begin{pmatrix} D \\ H \\ E_1 \\ E_2 \\ E_3 \end{pmatrix} \text{ and } \underline{Z}=\begin{pmatrix} V_{F_2} \\ V_{\bar{F}_3} \\ \bar{V}_{F_3} \\ V_{E_1} \\ V_{E_2} \\ V_{E_3} \end{pmatrix},$$

then the estimates $\hat{D}$ and $\hat{H}$ in the Mather's approach are given by

$$\begin{pmatrix} \hat{D} \\ \hat{H} \\ \hat{E}_1 \\ \hat{E}_2 \\ \hat{E}_3 \end{pmatrix}=(X'X)^{-1}X'\begin{pmatrix} V_{F_2} \\ V_{\bar{F}_3} \\ \bar{V}_{F_3} \\ V_{E_1} \\ V_{E_2} \\ V_{E_3} \end{pmatrix}.$$

Hence, on substituting the corresponding values from table 3. 6 for the three examples, we obtain

	Ex. 1	Ex. 2	Ex. 3
$\hat{D}$	−9.8374	29.386	−15.8642
$\hat{H}$	1.9143	50.434	17.4883
$\hat{E}_1$	21.2326	27.099	26.8483
$\hat{E}_2$	13.2005	27.089	27.6200
$\hat{E}_3$	11.4643	3.1754	3.2085

In the senior author's approach the estimates $\hat{D}$ and $\hat{H}$ are obtained by solving the following set of equations using the ordinary least square method.

$$\begin{cases} \frac{1}{2}D+\frac{1}{4}H+K_1\sigma^2=V_{F_2(c)} \\ \frac{1}{2}D+\frac{1}{16}H+K_2\sigma_2=V_{\bar{F}_3(c)} \\ \frac{1}{4}D+\frac{1}{8}H+\sigma^2=\bar{V}_{F_3(c)} \\ \sigma^2=\hat{\sigma}^2 \end{cases}$$

where $K_1=1+\frac{N_{F_2}}{rp(bN_{F_2}-1)}(b-1)$ and $K_2=\frac{p(a_1b-1)+a_1(b-1)}{rp(ba_1-1)}$

Hence, if we denote it by

$$X_1=\begin{pmatrix} \frac{1}{2} & \frac{1}{4} & K_1 \\ \frac{1}{2} & \frac{1}{16} & K_2 \\ \frac{1}{4} & \frac{1}{8} & 1 \\ 0 & 0 & 1 \end{pmatrix},\quad \theta_1=\begin{pmatrix} D \\ H \\ \sigma^2 \end{pmatrix},\quad \underline{Z}_1=\begin{pmatrix} V_{F_2(c)} \\ V_{\bar{F}_3(c)} \\ \bar{V}_{F_3(c)} \\ \hat{\sigma}^2 \end{pmatrix}$$

we obtain the estimates of D, H and σ^2 as $\begin{pmatrix} \hat{D} \\ \hat{H} \\ \hat{\sigma}^2 \end{pmatrix}=(X_1'X_1)^{-1}X_1'\underline{Z}_1$.

On substituting the relevant values from table 3. 6 for the three examples we obtain

	Ex. 1	Ex. 2	Ex. 3
$\hat{D}$	0.107	51.429	0.396
$\hat{H}$	−1.328	21.212	0.717
$\hat{\sigma}^2$	9.673	1.247	1.037

Comments

As the main purpose of the senior author's approach is to allow for a better control over the soil hetergeneity of blocks than that of Mathers, it might be expected that the senior auther's approach would be more efficient than that of Mather as regards the estimation of D and H. This is in fact evidenced from the results of the three generated examples, as given in the previous section.

From table 3. 6 it seems, however, that the efficiency of the senior author's method depends in turn on the values of σ^2, D and H. This may seem to be

Table 3. 6. *Comparison of the senior author's method with that of Mather as regards the estimation of D and H*

Ex. I

	Theoretical value	Mather's Method	Author's Method
D	0.5	−9.8374	0.107
H	0.18	1.9143	−1.3280
E_1		21.2326	
E_2		13.2005	
$E_3 (=\sigma^2)$	9.00	11.4643	9.673

Ex. II

	Theoretical value	Mather's Method	Author's Method
D	50.00	29.386	51.429
H	18.00	50.434	21.212
E_1		27.099	
E_2		27.989	
$E_3 (=\sigma^2)$	1.00	3.1754	1.247

Ex. III

	Theoretical value	Mather's Method	Author's Method
D	0.50	−15.9643	0.396
H	0.18	17.4883	0.717
E_1		26.8483	
E_2		27.6200	
$E_3 (=\sigma^2)$	1.0	3.2085	1.037

attributable to the adoption of the ordinary least square method. For it is well known that the efficiency of the estimates $\hat{\underline{\theta}} = (X'X)^{-1}X'\underline{Y}$ in $E\underline{Y} = X\underline{\theta}$ depends on the supposition of $V_{\underline{y}} = \sigma^2 I_n$. Since in both the senior author's approach and the Mather's approach this assumption is obviously not valid, the efficiency of both the senior author's and the Mather's Methods are therefore related to the degree of deviation of the variances of the Mather's statistics from the standart form $\sigma^2 I_n$. For large σ^2 such an inflation is expected to become appreciable, as evidenced from example 1, of the previous section.

From table 3. 6, while it is true that the senior author's method is less efficient for large σ^2 and small D and H (see results of example 1), it might be a useful method for small σ^2 and large D and H and large block differences (see results of examples 2 and 3). As noted in section two, the APBIB design

seems to be able to reduce σ^2 to some extend, the senior author's method may seem therefore worthy trying, especially when the block differences are big.

Summary

(a) In this paper three numerical examples were generated using the relevant parameters given in Table 3. 1 and employing a fixed model, together with the rules as specified in section 3. Using these generated data we compute the estimates of the genetic variances D and H in section 3 by employing the Mather's as well as the senior author's method as developed in (2). The results are given in Table 3. 6, which indicate that in all cases the senior author's method seems to be superior to that of Mather (1949) as regards the estimation of D and H. Such a result is to be expected since the senior author's approach may seem to allow for a better control over the soil hetererogeneity than that of Mather.

(b) While it might be true that the senior author's approach might be better then that of Mather for the estimation of genetic variances, it seems that the efficiency of the senior author's approach is also very low in case σ^2 is large while D and H are small. This is attributed to the adoption of the ordinary least square method whose efficiency is closely related to the degree of the deviation of the covariance matrix of $V_{F_2(c)}$, $V_{\bar{F}_3(c)}$, $\bar{V}_{F_3(c)}$ and $\hat{\sigma}^2$ from the standard form $\sigma^2 I_4$.

再論數量遺傳之分析方法

譚外元 魏書駁

(1) 本文第一作者曾提供另一方法籍以分析數量遺傳之資料。茲爲比較本文第一作者之方法與 Mather 方法起見，筆者等持利用常態逢機數字表及表 (3. 1) 之介量數值而構成三個實例如第三節所示。根據此三實例之計導結果顯示本文第一作者之方法一般均較 Mather 方法爲優。

(2) 根據表 3. 6 之結果，可見筆者之方法之效率與 σ^2, D 及 H 之大小有關。如 σ^2 甚大，則筆者之方法亦不如理想。究其原因可能爲由於使用通常之最小二乘方法以解 D 與 H 所以致。

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